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ANATOMICAL OBSERVATIONS OF THE SAND DOLLAR *MELLITA QUINQUIESPERFORATA* (LESKE, 1778) (ECHINODERMATA: ECHINOIDEA) AND THE DESIGNATION OF A NEOTYPE

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Abstract.—A neotype for the sand dollar *Mellita quinquiesperforata* (Leske, 1778) is designated and described. Quantitative and qualitative data are given for the test, spines, and pedicellariae of the neotype. Figures of plate and food groove patterns are also given for non-type specimens.

The genus *Mellita* L. Agassiz, 1841 comprises seven living species. Four occur only on the Pacific side of the Isthmus of Panama, and three on the Atlantic side (Harold & Telford 1990). *Mellita quinquiesperforata* (Leske, 1778), one of the Atlantic species, is the type species and most widely distributed member of the genus. In spite of its widespread occurrence, and its prominence in both appropriate habitats and shell shops, *M. quinquiesperforata* has a taxonomic history described as "strange" by Harold & Telford (1990:999). In their recent revision of the genus, Harold & Telford (1990) described this history, synonymizing *Mellita lata* Clark, 1940 and *Mellita latiambulacra* Clark, 1940 with *M. quinquiesperforata,* but raising *M. quinquiesperforata tenuis* Clark, 1940 to the status of species. For the *Mellita* occurring along the eastern coast of the United States, they named a new species, *Mellita isometra* Harold & Telford, 1990. These actions restricted the name *M. quinquiesperforata* to mainland populations occurring west of the Mississippi delta along the Central and South American coasts to southern Brazil, and to populations from some Caribbean Islands in association with terrigenous sand substrates.

The only reference to the deposition of the specimens in Klein's (1734) figures of *Mellita testudinata* (as pre-Linnean, this name is unavailable), upon which Leske's description of "*Echinodiscus quinquies perforatus*" is based, is "Hospitatur in museo Trieriano" (Leske 1778:198). At the time, the practice of designating type specimens was not well established, and it is even conceivable that Leske did not have the actual material in hand. Apparently, none of the earlier monographers of the genus (L. Agassiz 1841, Clark 1940, Mortensen 1948) made attempts to locate and examine Klein's specimens. Although Harold & Telford (1990:998) did make such attempts, they were "unable to ascertain whether or not these specimens still exist." There are currently no museums with natural history collections in Trier, Germany. Correspondence with the other museums that do exist there has failed to uncover the specimens. The importance of this species to studies in systematics, biogeography, ecology, and physiology compels us to designate a neotype. The name *Mellita quinquiesperforata* has been applied to a wide variety of taxa and used in many different senses. In particular, the eastern U.S. fossil *Mellita ampla* Ravenel, 1848 was placed in synonymy with *M. quinquiesperforata* by Harold & Telford (1990), but our preliminary examination suggests that *M. ampla* should be maintained as a separate taxon. Therefore, it is imperative that comparisons be made with types of both *M. quinquiesperforata* and *M. isometra.* Before these analyses can be done,

the name *M. quinquiesperforata* must be stabilized by designating and describing in detail a neotype.

Most aspects of the anatomy of *M. quinquiesperforata* remain poorly or not at all figured. This is particularly true for external appendages such as spines and pedicellariae, which are notably variable within and between species of clypeasteroids (Mooi 1989). Although presented under the name *Mellita quinquiesperforata,* the majority of previous figures are actually of *M. isometra,* the species most commonly encountered in marine laboratories of the eastern seaboard (for example, see Mooi [1986] and Telford et al. [1985] for spination and podia of *M. isometra*). Louis Agassiz (1841) recognized two species that are together synonymous with *M. quinquiesperforata.* He was the only one to figure spines of any kind from *M. quinquiesperforata,* in the sense of Harold & Telford (1990). Under the name of *M. testudinata,* Agassiz showed a single spine from the aboral margin of one of the lunules (L. Agassiz 1841: plate 4a, fig. 7a), although he does not indicate which one. Under the name *M. quinquefora,* he showed a poorly drawn club-shaped spine (L. Agassiz 1841: plate 3, fig. 11a) from the aboral surface, and three views of spines (L. Agassiz 1841: plate 3, figs. 11l, c, d) from the aboral margins of unspecified lunules. He described these spines as resembling elongated spoons, an observation that is not consistent with our own. Clark (1914: plate 125, figs. 16–21) figured several spines and pedicellariae from what he calls *M. quinquiesperforata,* but without knowing the locality of the specimen, or its appearance, it is impossible to know if this is indeed *M. quinquiesperforata,* or (as we suspect) *M. isometra.* In addition, Clark's figures are not especially accurate, and the figure of the "miliary spine" (Clark 1914: plate 125, fig. 16) seems to be a geniculate spine. A single bidentate pedicellaria from "*Mellita 5-perforata lata* H.L. Clark" was figured by Mortensen (1948), but it lacks detail in the tooth structure of the valves. No figures of biphyllous pedicellariae exist in the literature.

The plate pattern of the oral surface of *M. quinquiesperforata* from the "Gulf of Mexico" was figured by Durham (1955: fig. 17A). He also shows the basicoronal plate system (Durham 1955: fig. 16B). Unfortunately, there are errors in the positions and numbers of plate sutures associated with the anal lunule in Durham's drawing of *M. quinquiesperforata* (similar errors appear in his figure of *Leodia sexiesperforata* [Leske, 1778]). No figures of the plate pattern from the aboral surface exist in the literature, although some details can be made out in L. Agassiz's figure of *M. quinquefora* (L. Agassiz 1841: plate 3, fig. 1) and *M. testudinata* (L. Agassiz 1841, plate 4a, fig. 10). We could locate only 2 figures that unambiguously show the internal structure of *M. quinquiesperforata*: those in Mortensen (1948: plate 62, fig. 3) and Harold & Telford (1990: fig. 7). Only in the latter is the Aristotle's lantern visible.

Alexander Agassiz (1872) noted that *M. quinquiesperforata* "has a wide geographical range, and is liable to great variations." In the past, and in conjunction with taxonomic confusion stemming from these variations, it has been difficult to determine an unequivocal suite of characters for *M. quinquiesperforata.* For example, D. Pawson of the National Museum of Natural History, Washington, D.C. recently brought to our attention some difficulties in the use of Harold & Telford's (1990) key, particularly with respect to spine morphology, posterior paired lunule angle, and petaloid size. The present state of knowledge regarding the variation within the species suggests that the populations occurring in the northwestern Gulf of Mexico, including the type locality of Veracruz, Mexico, unequivocally belong to a single taxon. Harold & Telford (1990) pointed out that there was some distinctiveness of populations, particularly those

from islands in the Caribbean and from the southern parts of the range, but they preferred to recognize them only as geographic or ecophenotypic variants of *M. quinquiesperforata*. Some of these variants could turn out to be separate species, making it especially important to associate a specimen with the name *M. quinquiesperforata*. It is clear that a full description, especially of the spines, pedicellariae, and features of *M. quinquiesperforata*'s test architecture are necessary for adequate comparisons with types and other specimens of the rest of the species in *Mellita*.

Methods

Terminology of external appendages and test features is that of Mooi (1989), and the plate columns are labeled according to Lovén (1892). We provide an abbreviated synonymy, including all names that have been applied to *M. quinquiesperforata*. For references to more literature on this species, see Mortensen (1948) and Harold & Telford (1990). For a description, summary of intraspecific variation, and diagnosis of the species as a whole, see Harold & Telford (1990). Unless indicated otherwise, measurements are made directly from the neotype using dial calipers, with the value given in parentheses after each measurement representing percent test length. Additional comments are intended to cover anatomical aspects not emphasized by Harold & Telford (1990). Lunule angle is the number of degrees subtended by axes drawn through the lunules in ambulacra I and V. Spines and pedicellariae were removed from the test of the neotype and placed in droplets of approximately 5% sodium hypochlorite (Clorox). Fully cleaned spines were drawn using a camera lucida mounted on a compound microscope. Ten each of miliary spines (from aboral interambulacrum 2), aboral club-shaped spines (from aboral interambulacrum 2), geniculate spines (from oral ambulacrum I), locomotory spines (from oral interambulacrum 2), and anal lunule fringe spines (from the aboral edge at the mid-point of the lunule) were measured to the nearest μm using a calibrated eye-piece micrometer. To avoid damaging the neotype, specimens of similar size to, and collected with the neotype were prepared or dissected as follows. Plate patterns were made visible by polishing the specimen with a graded series of water-proof sand papers, and then painting the specimen with a light coat of a solution of equal parts glycerol and 95% ethanol. The plate patterns of both surfaces were drawn with the aid of a camera lucida mounted on a binocular dissecting microscope. The Aristotle's lantern was exposed through dissection of the aboral surface of another specimen and measured.

Order Clypeasteroida L. Agassiz, 1835
Family Mellitidae Stefanini, 1911
Genus *Mellita* L. Agassiz, 1841
Mellita quinquiesperforata (Leske, 1778)
Figs. 1–3

Echinodiscus quinquies perforatus Leske, 1778:197, pl. 21C, D.

Echinus pentaporus.—Gmelin, 1788:3189.

Clypeaster pentaporus.—Lamarck, 1801: 349.

Scutella quinquefora.—Lamarck, 1816:9.

Scutella pentapora.—Blainville, 1830:223.

Mellita quinquefora.—L. Agassiz, 1841:36, pl. 3 (plate is erroneously labelled "*Encope pentapora*").

Mellita testudinata.—L. Agassiz, 1841:40, pl. 4a, figs. 7–9.

Mellita nummularia.—L. Agassiz & Desor, 1847:139.

Mellita testudinea.—Gray, 1855:22.

Mellita pentapora.—Lütken, 1864:107.

Mellita quinquiesperforata.—H. L. Clark, 1911:599.

Mellita quinquiesperforatus.—H. L. Clark, 1925:174.

Mellita lata.—H. L. Clark, 1940:437, pl. 60, fig. 1, pl. 61, fig. 1, pl. 62, figs. 1, 2.

Mellita latiambulacra.—H. L. Clark, 1940: 439, pl. 62, figs. 3–6.

Mellita quinquisperforata var. *latiambulacra.*—Penchaszadeh & Layrisse, 1985: 393.

Neotype.—California Academy of Sciences, Invertebrate Zoology (CASIZ) 096152, 44.2 mm test length, beach 2 mi south of Veracruz, Mexico, A. G. Smith, March 1954 (collected with CASIZ 087802, geology accession number 34684, 11 specimens in lot not counting neotype, ranging from 26.6 mm to 44.6 mm test length).

Description of neotype.—Test dimensions (Fig. 1): Length 44.2 mm; maximum width 48.0 mm (108.6%); distance from ambitus at ambulacrum III to anterior edge of madreporic plate 19.4 mm (43.9%); test thickness at center of madreporic plate 5.6 mm (12.7%); test thickest anterior to madreporic plate, thickness at highest point 5.9 mm (13.3%); distance from ambitus at ambulacrum III to highest point of test 13.2 mm (29.9%); distance from ambitus at ambulacrum III to anterior edge of peristome 13.0 mm (29.4%); mouth diameter 2.0 mm (4.5%); distance from anterior edge of peristome to anterior edge of periproct 4.0 mm (9.0%); periproct indenting basicoronal, in depression leading to anterior edge of anal lunule, length 1.9 mm (4.3%).

Petaloids (Fig. 1A): Only a single trailing podium in each of petaloids Ib, IIb, IIIa, IVa and Va (see also Fig. 3). Following measurements represent length of indicated petaloid pore pair column in ambulacra: Ib 11.2 mm (25.3%); IIb 10.00 mm (22.6%); IIIa 11.3 mm (25.6%); IVa 11.0 (24.9%); Va 11.7 mm (26.5%). Following measurements represent greatest width of petaloid in ambulacra: I 5.4 mm (12.2%); II 5.2 mm (11.8%); III 5.0 mm (11.3%); IV 5.1 mm (11.5%); V 5.5 mm (12.4%).

Food grooves: Primary grooves bifurcate on, or just distal to ambulacral basicoronal plates; two main branches in each ambulacrum restricted to ambulacral plates; distal, secondary branches extend onto interambulacral plates (see also Fig. 3). Following measurements represent greatest distance (orthogonal to lunule axis) between main branches of food grooves in ambulacra: I 9.5 mm (21.5%); II 10.1 mm (22.9%); III 6.3 mm (14.3%); IV 10.0 mm (22.6%); V 9.3 mm (21.0%).

Lunules (Fig. 1): Lunules closed. Following measurements represent lengths and widths respectively of lunules in ambulacra: I 8.4 mm (19.0%) and 1.7 mm (3.8%); II 8.6 mm (19.5%) and 1.7 mm (3.8%); IV 7.7 mm (17.4%) and 1.8 mm (4.1%); V 8.4 mm (19.0%) and V 1.7 mm (3.8%); lunule angle 73.5°; distance from anterior edge of madreporic plate to anterior edge of anal lunule 6.6 mm (14.9%); length and width of anal lunule 11.8 mm (26.7%), 2.5 mm (5.7%).

Spines (Fig. 2): Measurements given here are mean spine lengths, followed by (in parentheses) range and standard deviation. Aboral miliary spines (Fig. 2A) slender, bent at base so that whole spine leans "down-slope" from apical system, distal end with typical sac-bearing tip architecture (see Mooi 1986), length 508.2 μm (486–528, 11.8). Aboral club-shaped spines (Fig. 2B, C) fairly stout, with thick shaft bent at base so that whole spine leans "down-slope" in manner similar to aboral miliaries, tip moderately expanded and club-shaped, length 642 μm (605–658, 15.0). Geniculate spines (Fig. 2D) of oral surface slender and sharply bent just distal to point half way up shaft, length 572 μm (546–598, 18.5). Locomotory spines (Fig. 2E) of oral surface long, slender, sharply bent proximal to base, moderately pointed, length 2397 μm (2073–2611, 153.0). Anal lunule fringe spines (Fig. 2F) from aboral edge of lunule paddle-shaped, but broadest and most greatly flattened at lunule's mid-point, shaft proximal to base slightly bent in same plane as flattening, tip

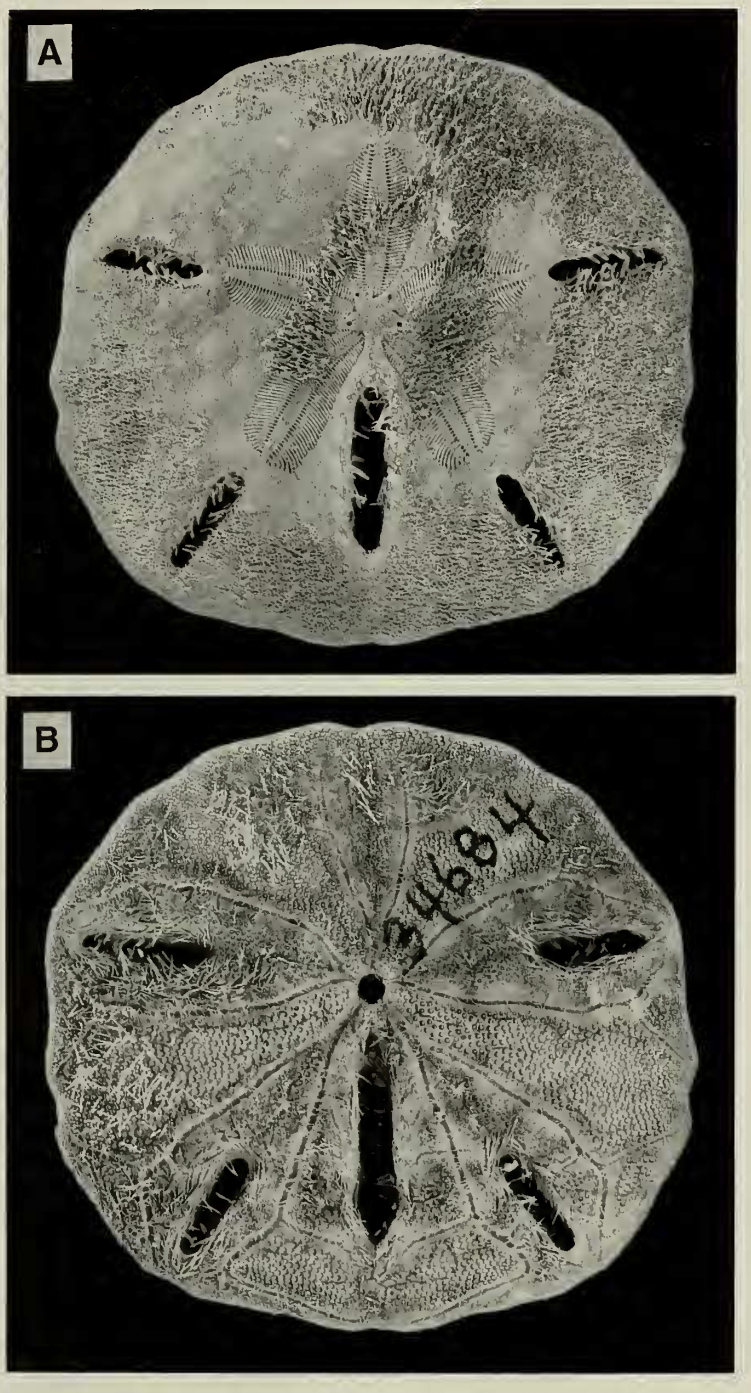

Fig. 1. *Mellita quinquiesperforata,* neotype (CASIZ 096152, 44.2 mm test length). A. Photograph of aboral surface; B. Photograph of oral surface.

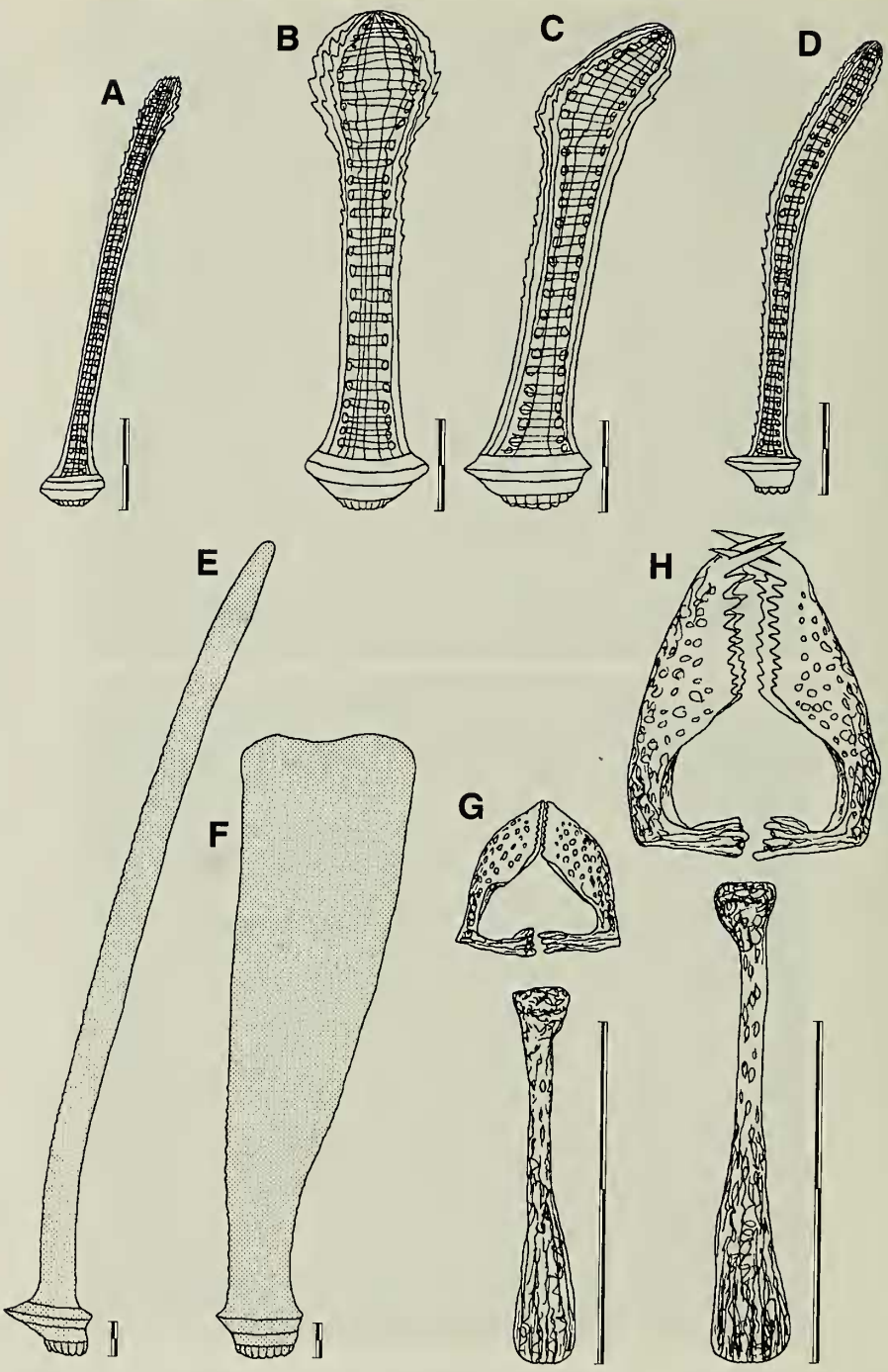

Fig. 2. *Mellita quinquiesperforata,* neotype (CASIZ 096152), skeletal elements of external appendages. A. Miliary spine from interambulacrum on aboral surface, apex left; B. Club-shaped spine from interambulacrum on aboral surface; C. Club-shaped spine from interambulacrum on aboral surface, view orthogonal to that in B, apex left; D. Geniculate spine from ambulacrum on oral surface; E. Locomotory spine from interambulacrum on oral surface, details of stereom structure omitted; F. Anal lunule fringe spine from aboral edge at mid-point

chisel-like and square, length 1610 μm (1370–1772, 115.8).

Pedicellariae (Fig. 2): Pedicellariae of two types, both with two valves forming a "jaw" attached to stem by long, flexible neck of almost same length as stem. Valves of biphyllous pedicellariae (Fig. 2G) with minute teeth all of similar size, valve length approximately 45 μm. Stem slender, tapering distally but ending in slight swelling, stem length approximately 110 μm. Valves of bidentate pedicellariae (Fig. 2H) with variably sized teeth, 2 or 3 long, distal "canine" teeth on a valve interlocking with those of opposing valve, valve length approximately 95 μm. Stem slender, same general shape as for biphyllous, stem length approximately 140 μm.

Plate pattern (Fig. 3), Aristotle's lantern of non-types.—Aboral plating around ambulacral lunules festooned except in ambulacrum III, which lacks lunule. Aborally, narrowest point of interambulacrum 5 posterior to anal lunule. At ambitus, interambulacra and ambulacra approximately same width. Orally, interambulacra discontinuous by single ambulacral plate except for interambulacrum 5, which is continuous. During ontogeny, last post-basicoronal plates to become disjunct from their corresponding basicoronals are those in interambulacra 1b, 2a, 3b and 4a. Four interambulacral plates form perimeter of anal lunule on oral surface, two circumferential sutures close to posterior end of lunule. Interambulacral basicoronal plates longer than ambulacral basicoronals. Interambulacral basicoronal 5 deeply indented by periproct. In specimen 42.5 mm long, Aristotle's lantern 8.8 mm long (20.7% test length).

Remarks.—Klein (1734) described and figured specimens of this species from Veracruz and Leske (1778), the first post-Linnaean writer to describe *M. quinquiesperforata* (as *Echinodiscus quinquies perforatus*) referred specifically to Klein's figures (Harold & Telford 1990). Accordingly, we have chosen a specimen from a lot from Veracruz as the neotype. The neotype does not differ significantly from the material examined by Harold & Telford (1990). How-

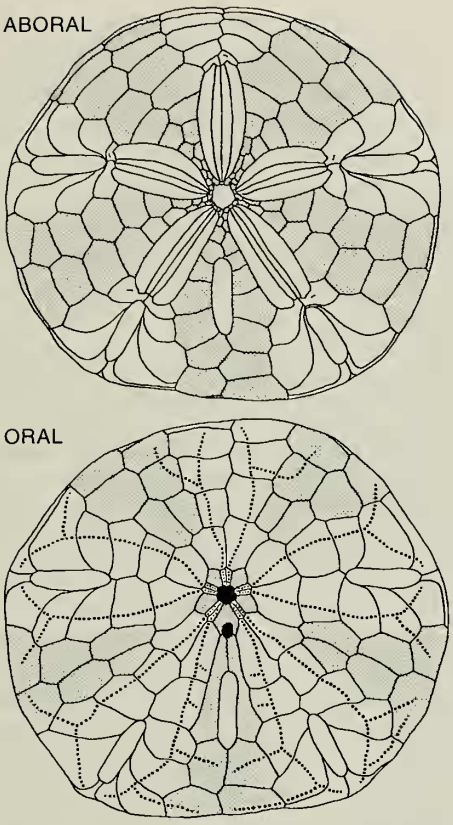

Fig. 3. *Mellita quinquiesperforata* (CASIZ 087802, 44.6 mm test length, collected with neotype), plate and food groove patterns. Food grooves represented by dotted lines, details of plating in petaloids omitted. Mouth and periproct in solid black, interambulacral plates shaded.

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of anal lunule, details of stereom structure omitted; G. Valves (upper) and stem (lower) of biphyllous pedicellaria; H. Valves (upper) and stem (lower) of bidentate pedicellaria. All scale bars 100 μm long.

ever, as noted by Harold & Telford (1990), there is substantial variation within *M. quinquiesperforata,* particularly in width to length ratio, profile, and spine dimensions. In spite of previous attempts to do so (for example, see Clark 1940), Harold & Telford (1990) could find no basis upon which to partition this variation into species. We concur based on the characters examined by previous authors as well as on new observations (D. Pawson, A. S. Harold, & R. Mooi, unpublished observations). The neotype here designated not only comes from the type locality, it also exhibits the sharply inclined anterior profile, anteriorly placed site of maximum thickness, very broad test, and spatulate spines bordering the lunules listed in Harold & Telford's (1990) diagnosis. Although pedicellarial types can be diagnostic of certain clypeasteroid clades (Mortensen 1948, Mooi 1989), the pedicellariae of the neotype illustrated here (Fig. 2) are typical not only of *Mellita quinquiesperforata,* but of the genus as a whole, and do not offer additional taxonomic information.

The neotype typifies the apomorphies shared by *M. quinquiesperforata* and other *Mellita.* Phylogenetic revision of fossil *Mellita* (R. Mooi & A. S. Harold, unpublished observations) indicates that *Leodia sexiesperforata* is a member of the clade encompassing both fossil and extant *Mellita* species. Taking this into account, the apomorphies of *Mellita* include a single trailing podium at the end of each petaloid, and the periproct indenting the basicoronal plate. Harold & Telford (1990) added the loss of the lunule in ambulacrum III to this list. However, this character is actually applicable only to a smaller clade of largely extant *Mellita,* and not to the genus as a whole (R. Mooi & A. S. Harold, unpublished observations). Our examination of the neotype and associated material also affords an opportunity to rectify Durham's (1955) error in interpretation of the plate patterns around the anal lunule (compare our Fig. 3 with Durham 1955: fig. 17A).

A survey of spine morphometrics within the Mellitidae (D. Pawson, A. S. Harold & R. Mooi, unpublished observations) reveals unexpected divergences from the characters given in the key by Harold & Telford (1990). They use the relative lengths of anal lunule fringe spines and locomotory spines in their first couplet: in *M. tenuis* and *M. isometra,* the anal lunule fringe spines are supposed to be "substantially longer" than the locomotories. In all other *Mellita,* the reverse is the case. The anal lunule fringe spines are shorter than the locomotories in the neotype and other examples of *M. quinquiesperforata* and is therefore in accord with Harold & Telford's key. However, with the recognition that some populations of *M. isometra,* and perhaps of *M. tenuis,* have longer locomotories than anal lunule fringe spines, more comprehensive study of intraspecific variation (including all available types) is essential to assess the systematic, environmental, and ontogenetic significance of previously unrecognized variation in relative spine lengths.

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